Preference consistency relies on hippocampal function:

Evidence from mediotemporal lobe epilepsy

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# Introduction

It seems obvious that our preferences draw on past experience and hence memory. Memory representation of past choices and their consequences allow us to learn what sources of food provide optimal nourishment and which predators and other dangers should be avoided, ensuring our survival and well-being. Confronted with a choice of snack food items at a vending machine, we use the packaging as memory cues to retrieve past experiences with the options to construct an estimate of their reward value.

In contrast, economics treats preferences as a primitive in axiomatic models of risky choice (Von Neumann & Morgenstern, 1944). As a result, the connection between properties of memory and judgment and choice has historically been neglected, with only a few exceptions (Elke U. Weber, Goldstein, & Barlas, 1995). More recently, memory processes and constraints have played a more prominent role in explanations of decision-making phenomena, in an attempt to leverage what we know about memory to explain well-known decision phenomena (Dougherty, Gettys, & Ogden, 1999; Reyna, Lloyd, & Brainerd, 2003; Schneider & Shanteau, 2003; Elke U Weber & Johnson, 2009).

Memory processes provide entry points for psychological models of judgment and choice that have the potential to more accurately describe observed judgments and decisions. Previous incorporation of attentional and perceptual processes has resulted in models such as prospect theory (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992) that have succeeded to account for response patterns considered anomalies by rational choice models such as expected utility theory.

If preferences are often constructed (see Lichtenstein & Slovic, 2006), an insight that may arguably be psychology’s most successful export to economics, then memory processes can be expected to play a major role in this construction. Both memory encoding and retrieval processes influence judgment and choice in multiple ways (see Weber & Johnson, 2009 for a review). Query theory (Johnson, Häubl, & Keinan, 2007; E U Weber et al., 2007) suggests that decision-makers consult their memory (or external sources) with automatic and implicit queries about the choice alternatives, in particular arguments for choosing one or the other, i.e., their merits or liabilities. Past experiences and other associations provide the basis for such evaluation.

Parallel lines of investigation in neuroscience have focused on the Prospective Memory network. Here it has been shown that future-oriented episodic imagery, i.e. the mental construction of specific future events based on past experience, influences intertemporal choices. Stronger activity in this prospective memory network, including the hippocampus, is associated with decreased temporal discounting of monetary rewards (Benoit, Gilbert, & Burgess, 2011; Peters & Büchel, 2010). Wimmer & Shohamy (2012)showed that the MTL is also involved in the transfer of value of rewarded stimuli by associative learning and how these memory mechanisms bias decisions. A recent study highlighted the involvement of the MTL in preference-based choices. When preferences for novel food items had to be explicitly constructed from two familiar, previously uncombined tastes, the hippocampus as well as the medial prefrontal cortex provided value information (Barron, Dolan, & Behrens, 2013).

One way of demonstrating that memory representations of past experience play a role in choice is to show that choice is impaired in individuals who are known to have memory encoding or retrieval deficiencies. Memory of past experiences and imagining future experiences activate a common set of brain regions that include the hippocampus (Schacter & Addis, 2007), and these functions are impaired in patients with hippocampal damage (Hassabis, Kumaran, Vann, & Maguire, 2007; Klein & Loftus, 2002).Thus patients with hippocampal sclerosis may be expected to show impaired preference construction.

To test this hypothesis, we employ a simple paradigm, a series of binary choices among simple food products. Our measure of choice quality is the transitivity of preference, i.e., whether or not preferences for different options are consistent across choice pairings. For example if a person chooses A over B, and B over C, transitivity requires that they must pick A over C (Samuelson, 1938). Transitivity has been a central measure in early work in decision-making (Tversky, 1969), and recent work examining preferences in neuroscience (Camille, Griffiths, Vo, Fellows, & Kable, 2011; Fellows & Farah, 2007; Fellows, 2006; Kalenscher, Tobler, Huijbers, Daselaar, & Pennartz, 2010) and consumer choice (Lee, Amir, & Ariely, 2009). One reason for focusing on transitivity is that it is central to the General Axiom of Revealed Preference and is necessary and sufficient for value maximization (Houthakker, 1950). Transitivity of preferences is embraced by most individuals as a desirable property of a choice process. Most people will change intransitive choice patterns to transitive ones, when their inconsistencies are pointed out to them (Birnbaum & Gutierrez, 2007).

Research using patients with lesions in the ventromedial frontal lobe, in areas known to be involved in the expression of value, showed a greater frequency of intransitivities for choices between gambles (Camille et al., 2011) and for preferences for food, colors, and people (Fellows & Farah, 2007). The latter study included an important control: An increase in intransitivity was not observed for perceptual judgments, suggesting that preferential tasks were uniquely affected.

We adapt the paradigm but examine the effect of damage to the hippocampus, an area not known to be involved in the expression of value but, according to our hypothesis, involved in the generation of input to any value calculation. In particular, our task examines binary choices among pairs of 20 commonly available candy bars, a product we could expect to be familiar and interesting to participants. We also included a control judgment, asking respondents to judge which of two numbers was bigger. In both cases our dependent measure was the transitivity of (preference or magnitude) judgments.

# Methods

Thirty-one patients suffering from mesial temporal lobe epilepsy with clinically diagnosed uni (left:n=14;right:n=8) - or bilateral (n=9) hippocampal sclerosis from the presurgical program at the Department of Epileptology in Bonn were included in the study (MTL). Two control groups consisted of thirty patients with extratemporal lobe epilepsy (ETL) and thirty healthy control subjects (CON), respectively. The study was approved by the local ethics committee of the University of Bonn and the Institutional Review Board at Columbia University (IRB-AAAB1301) and all subjects gave their written informed consent. The three groups did not differ with respect to age or gender (see Table S1 for details).

# Behavioral experiment

Each subject made a series of binary choices on a computer between pairs of candy bars, each represented pictorially as shown in Fig.1, drawn randomly out of a set of twenty, with each combination presented once, resulting in 190 choices. This procedure was similar to that used to examine the effect of ventromedial frontal lobe damage on choice used by Camille et al. (2011), Fellows & Farah (2007) and Fellows (2006), and used familiar candy bars as the choice objects (see also Lee et al., 2009). A choice triplet was counted as inconsistent, if chocolate bar “A” was preferred over “B” and “B” over” C”, but “C” was preferred over “A”. In a control task, subjects were presented with numbers from one to twenty and had to judge which number was larger. Judgment inconsistency in triplets of magnitude was computed identically. Subjects knew that they would receive their choice from one randomly selected candy bar choice trial, in addition to a participation fee of 10 €.



Fig 1. Three trials of the binary choice experiment. Subject indicated their preferred candy bar on each trial. The timing of the stimulus presentation and choice was self-paced, with a maximum length of 5 seconds.

# MR sequence and analysis

For a subgroup of the patients with unilateral hippocampal sclerosis (n=16), a 3D-T1 weighted high-resolution data set (MP-RAGE, voxel size 1x1x1mm, repetition time 1570ms, echo time 3.42ms, flip angle 15°, field of view 256mm x 256mm) was available for volumetric measurement of the hippocampus. This was done in a fully automated manner by means of the FreeSurfer image analysis suite (Version 5.1.0, Martinos Center, Harvard University, Boston, MA, U.S.A.) (Fischl et al., 2002, 2004), which is documented and freely available for download online (<http://surfer.nmr.mgh.harvard.edu/>). Because of the high variance in hippocampal volume between individuals, we used a lateral damage index of hippocampal volume to express the extent of unilateral hippocampal damage in our MTL group:

This lateral damage index can obviously by only assessed for subjects with unilateral hippocampal sclerosis.

# Statistical analysis

Statistical analyses were performed using SPSS Statistics 21.0 for Windows (IBM, Armonk, NY, U.S.A.) and R (Version 3.0.2) for Mac. We use a two-tailed p-value of 0.05 as our criterion for statistical significance and mark significant differences in the figures and tables with asterisks: \*p ≤ 0.05, \*\*p ≤ 0.01, and \*\*\*p ≤ 0.001.

## Tallying intransitivities

The binary choices made by each subject were transformed into a matrix of triplets, as the detection of intransitivity requires three choice pairs. Each matrix consisted of 1140 rows, representing all possible combinations of 3 of 20 bars. A triplet was marked as indicating intransitivity either if A was chosen over B and B was chosen over C yet C was chosen over A or if B was chosen over A and C was chosen over B yet A was chosen over C:

or

The proportion of intransitive choices was obtained by dividing the number of intransitive triples by the total number of triples. This provided the central dependent measure.

# Results

Patients with hippocampal sclerosis showed an increased number of intransitive choices compared to the two control groups (Fig. 2; mean percentages: MTL: 6.21%; ETL: 3.47%; CON: 2.75%; median percentages: MTL: 4.56%; ETL 2.81%; CON: 2.94%) Kruskal-Wallis-Test of independent groups p<0.001). The two controls group did not differ significantly in intransitivity from each other (Wilcoxon rank sum test p = 0.78), but both groups differed significantly from the MTL group (MTL vs ETL p = 0.02, MTL vs CON p <.001, Bonferroni adjusted). Very similar results are provided by an Analysis of Variance with post-hoc comparisons (p < .001).

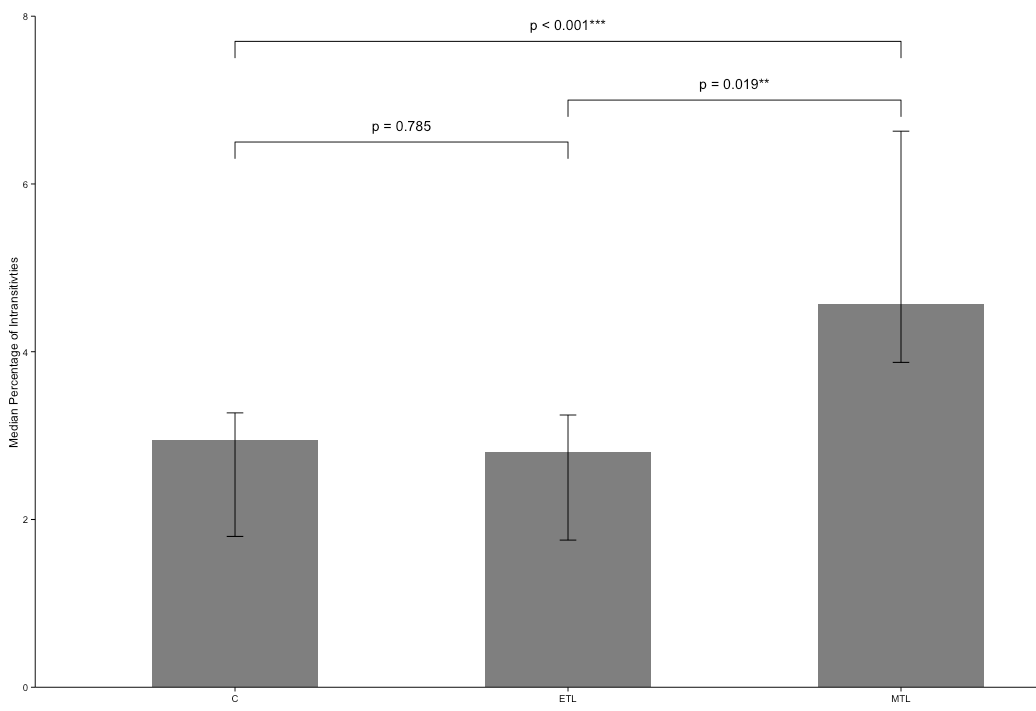


Fig 2.Median percentage of intransitives per group. Group comparisons computed Wilcoxon rank sum test and 95% confidence intervals calculated from bootstrapped medians from 2500 samples.

Consistent with our hypothesis that hippocampal retrieval of candy bar associations acquired over respondents’ prior life was used in preference construction and choice, we found that the ratio of compromised hippocampal volume to total volume was significantly correlated with the amount of choice inconsistencies (Fig.3; spearman-rho = 0.761; p<0.001; n=16).

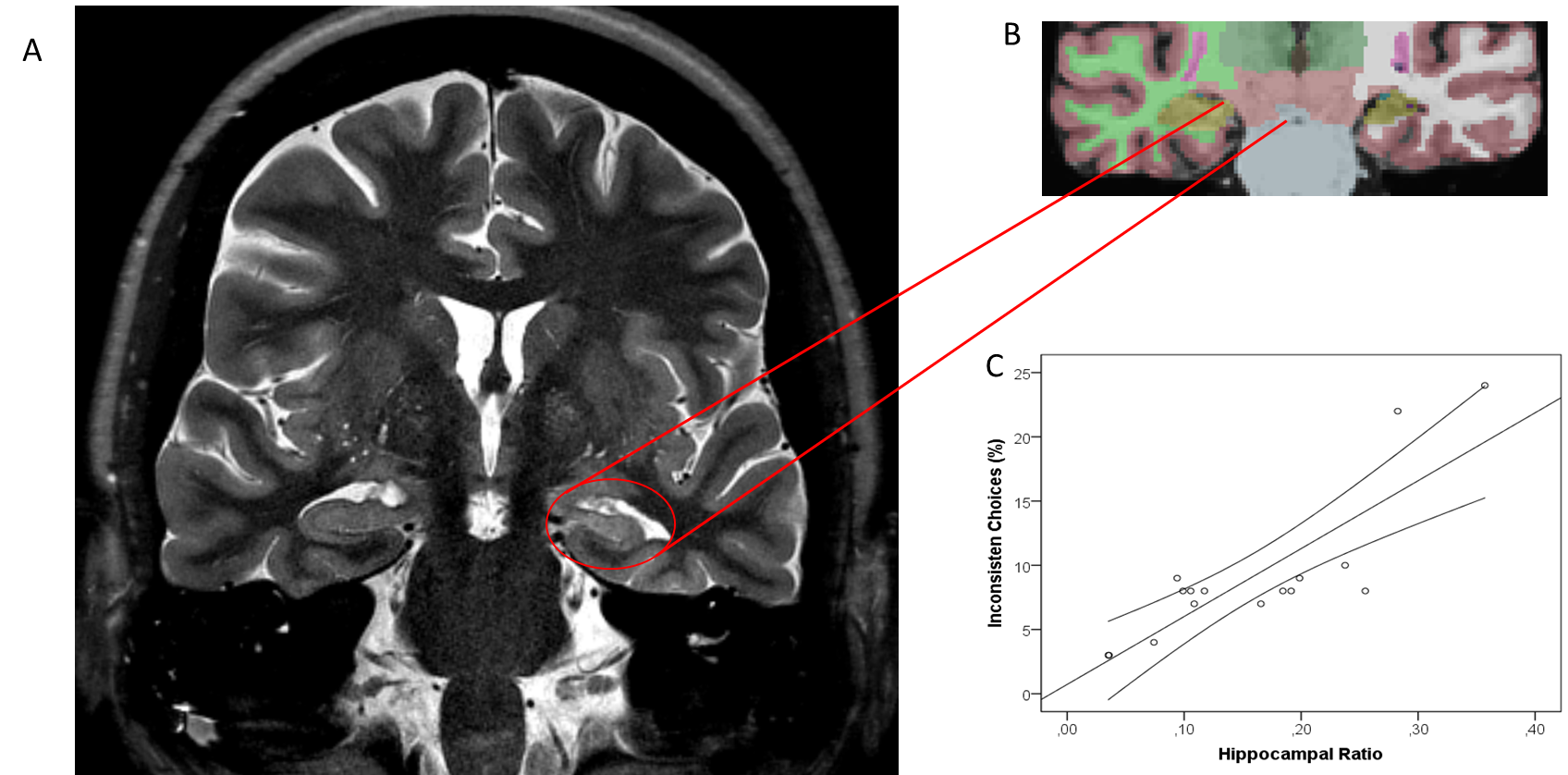


Fig 3. Example of a typical hippocampal sclerosis on a T2-weighted image (A), automated hippocampal volumetry (B) and correlation of hippocampal asymmetry (as a marker for unilateral atrophy) and percentage of inconsistent choices with 95% CI of the mean. rho=0.761, p<0.001

To rule out alternative explanations, in particular the possibility that subjects may have explicitly remembered their previous choices within this study, using this information to avoid intransitivities, and that it is this ability that may be impaired in patients with hippocampal damage, we examined if the observed group differences in choice inconsistencies were stable across the course of the study session. Although each pair of options is seen only once, prior choices involving one of the two candy bars might influence subsequent choices, and memory for these choices might differ across groups, with the MTL group being less able to retrieve their choices on earlier trials. This alternative explanation for the observed group differences in transitivity suggests that more intransitivities should occur later in the session, particularly for the MTL group. We tested this hypothesis by examining for differences in the effects of trial on the frequency of intransitivities across groups. As detailed in the SOM, no differences were found.

To examine the possibility of a speed-accuracy tradeoff, we also examined response latencies of the choices, and the relationship between responses latencies and intransitivities. We found that slower trials were most likely to be involved in intransitive triplets, and that the MTL group has a significantly slower average response time per trial. Together, these results suggest that intransitive triplets accompany more careful, longer responding, eliminating the possibility of a speed-accuracy tradeoff.

We also examined whether particular options were responsible for intransitivies. We regressed the number of times each trial was involved in an intransitive choice onto indicator variable representing the identity of each chocolate bar as well a factor representing group. None of these variables survived a post-hoc (Bonferroni) test of significance. Furthermore we calculated the utilities of each bar for each subject and checked whether the difference in utilities predicted how often a pair was involved in an intransitivity. Expectedly those that were closer in value were more likely to lead to intransitivity.

To ensure that the intransitives we observe are associated with reporting preferences, we examined performance in the control task. In the control task, respondents identified which of two numbers was larger. All groups did well, though the ETL group was significantly worse than the control group (percentage of errors: MTL: 0.81%; ETL: 1.09%; CON: 0.07%; p<0.001 Kruskal-Wallis test for independent groups; MTL vs. ETL n.s.; MTL vs. CON n.s; ETL vs. CON p<0.05) and ETL patients exhibited a much higher variance in this task. The absence of a difference in inconsistency between the MTL and the control groups in this task and the presence of a differences in choice inconsistency supports the involvement of hippocampal function in preference based choices and not more general attentional effects.

# Discussion

There is increasing interest in how value representations are constructed. In this paper we provide support for the role of memory in preference construction, by showing that hippocampal lesions are associated with an increase in intransitive preferences and that the degree of intransitivity is related to magnitude of the damage to the hippocampus. A control task not involving preference-based choices does not show these effects, nor do respondents who have lesions outside of the medial temporal lobe. These results implicate the hippocampal areas in preference construction.

Our hippocampal patients produce patterns of intransitivity of preference that are strikingly similar to those observed in ventromedial prefrontal cortex (vmPFC) patients, suggesting that the associations and memories stored in the hippocampus may serve as inputs to value calculation occurring elsewhere (Barron et al., 2013). The hippocampus is one of the most highly interconnected brain areas, including a direct monosynaptic connection to the prefrontal cortex (Cole, Pathak, & Schneider, 2010; Godsil, Kiss, Spedding, & Jay, 2013; Ongür & Price, 2000). Ranganath and Ritchey (2012) proposed a division of the MTL into two systems for memory-guided behavior: the anterior (AT) and posterior-medial (PM) system. The AT, which is comprised of the peri-rhinal cortex and anterior parts of the hippocampus and amygdala has strong interconnections with the frontal cortex, has been argued to be involved in familiarity-based cognition, social behavior and saliency. Ranganath & Ritchey (2012) suggest that “the AT system could facilitate the construction of knowledge about people, so that past experiences can be used to inform inferences about the personality and intentions of others, irrespective of their behavior in a particular context.” Our results suggest that this connection to the ventromedial prefrontal cortex may also serve the construction of preferences. Fellows (2006) showed that vmPFC lesioned patients differ from normal controls in their external information search, in ways that could be attributed to diminished planning capacity. Perhaps retrieval of experiences from memory is also inhibited in vmPFC patients, but this is an interesting topic for future research.

Some early judgment and decision making research used the existence of specific forms of intransitive preferences as evidence for choice rules that differ from value maximization (Tversky, 1969), with some recent criticisms (Regenwetter, Dana, Davis-Stober, & Guo, 2011) that argue that deviations of choice patterns from value maximization may be due to simpler reasons, including changing preferences and indifference.  Our work uses intransitivities in a much simpler way, namely as evidence that preferences are less stable in decision makers whose MTL regions have been impaired. We also show that the degree of preference instability is a function of the degree of hippocampal damage.

The amount of intransitivities we observe, although significantly increased in patients with hippocampal damage, is still far from showing a size expected if just random values were retrieved. Simulating the effect of noise on the level of intransitivity shows that the observed inconsistency levels correspond to roughly 25% of noise added to a completely transitive set of preferences (see SOM for details).

Several interpretations laying ground for future research may underlie these observations: i) the hippocampus is just one part in a larger network of relevant brain areas involved in the retrieval and processing of choice values. A recent review of Shohamy and Turk-Browne nicely reviews the evidence of hippocampal involvement in a variety of cognitive functions outside of the domain of declarative memory. It suggest two different hypotheses of hippocampal function; the memory modulation hypothesis proposes that representations within the hippocampus may transiently bias other cognitive functions such as value computations in the present task. The adaptive function hypothesis on the other hand highlights the hippocampus as a central processing unit with specific computations carried out in the hippocampal networks, depending on the task at hand (Shohamy & Turk-Browne, 2013). Both models of hippocampal functions, though, would be in line with our findings of only small disturbances in contrast to random choice behavior.

ii) compensation mechanisms might be involved in patients with chronic hippocampal lesions. It is well known that chronic brain lesions may lead to compensatory shifts in neural processes, e.g. in the domain of language processing (Kipervasser et al., 2008; B. Weber et al., 2006). The application of neuroimaging methods, like functional MRI, during a value-based decision task in these patients could be used to investigate compensation mechanisms in future research.

A third explanation could be remaining functions within the affected hippocampus. Although patients with temporal lobe epilepsy and hippocampal sclerosis do show neuropsychological deficits especially in the domain of declarative memory, the amount to which these deficits occur varies strongly between patients and they hardly show amnesic behavior(Hoppe, Elger, & Helmstaedter, 2007). Future research combining in-depth neuropsychological testing together with value-based choice tasks may shed light on the specific cognitive components relating to the observed decision deficits.

Our results suggest a critical role for the hippocampus as the carrier of input into the construction of the value of choice options. Most decisions require the construction of value based on past experience: Even a previously experienced option, like a favorite dish in a familiar restaurant, requires us to compare that option to newly available options (dinner specials). Combining what we know about internal and external inputs to preference construction processes and about information aggregation and comparison will allow us to better understanding how the brain calculates value and makes wise choices.

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